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GENERIC LIMITS IN THE TRIBE CLADOTHAMNEAE (ERICACEAE), AND ITS POSITION IN THE RHODODENDROIDEAE

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THE CLADOTHAMNEAE COMPRISE a group of four species, all ornamental shrubs, in the Ericaceae subfamily Rhododendroideae. Although they are all fairly well known, being in cultivation, the four species have been given four generic names. There is no consistency in the usage of these names, as the arrangements listed below indicate.

SPECIES EPITHET	*racemosa*	*paniculata*	*bracteata*	*pyroliflorus*	REFERENCE
GENERIC PLACEMENT	***Elliottia***	*Elliottia*	*Elliottia*	*Cladothamnus*	Hooker, 1876; Copeland, 1943
	Elliottia	*Elliottia*	*Botryostege*	*Cladothamnus*	Stapf, 1934
	Elliottia	*Tripetaleia*	*Tripetaleia*	*Cladothamnus*	Drude, 1897; Cox, 1948
	Elliottia	*Tripetaleia*	*Tripetaleia*	*Tripetaleia*	Stevens, 1971 (combination of *C. pyroliflorus* in *Tripetaleia*, not published)

In the following discussion, Copeland's nomenclature will be followed.

This paper is an attempt to resolve the generic limits in the group by using evidence from anatomy, chemistry, morphology, and palynology,[1] and combining this information with what is already known about floral anatomy. The evidence presented here suggests that there is only a single

[1] The sections of morphology and anatomy are by Brim and Stevens; the former examined the group during the course of his work for a Senior Thesis at Harvard University. Bohm has a long-standing interest in the flavonoids of the group, while the pollen was examined by Hebda in conjunction with the work of the other authors. The introduction and general discussion, written by Stevens, are acceptable to all.

genus, *Elliottia*, and it also provides a firmer basis for understanding the phylogeny of the Ericaceae subfamily Rhododendroideae as a whole.

The Cladothamneae were first recognized as a separate tribe within the Rhododendroideae by Copeland (1943) on the basis of evidence from morphology, floral anatomy, and embryology. Four species were included: *Cladothamnus pyroliflorus* Bongard, from northwestern North America (MAP 2); *Elliottia racemosa* Muhl. ex Elliott, from southeastern North America (MAP 3); and *E. paniculata* (Siebold & Zucc.) Bentham & Hooker f. and *E. bracteata* (Maxim.) Bentham & Hooker f., both from Japan (MAP 1). A fifth species, *Tripetaleia yakusimensis* Nakai, has been described from Japan, but it was considered by Kyôgoku (1962) to be a synonym of *T. paniculata* Siebold & Zucc. (*E. paniculata*). On the basis of numerical analysis, Watson, Williams, and Lance (1967) suggested that the species that they studied (*C. pyroliflorus*, *E. paniculata*, and *E. bracteata*) would be better included in the Rhodoreae D. Don. Stevens (1971) followed Copeland in his circumscription of the Cladothamneae. Whether placed in a separate tribe or not, the four species included in the Cladothamneae are clearly more closely related to one another than they are to any other members of the Rhododendroideae.

Ericaceae subfamily Rhododendroideae tribe **Cladothamneae** Copeland.

Shrubs or small trees. Indumentum of unicellular hairs only, plant sometimes almost glabrous. Leaves deciduous, convolute in bud, entire. Inflorescence terminal, ± monotelic (cymose), eperulate; ± foliaceous bracts and "bracteoles" usually present, the former sometimes occurring alone, without the latter; pedicel continuous with the calyx. Flowers 3- to 5-(or 6-)merous; calyx well developed, the sepals connate or free; corolla polypetalous; stamens 5 to 10, the filaments flattened, the anthers with resorption tissue, dehiscing by long slits, the pollen shed in very young bud, the tetrads with viscin threads; ovary glabrous, 3- to 5-locular, placentation axile, the placentae apical; style impressed into the apex of the ovary, with an expanded collar around the ± prominent stigma. Capsule septicidal; seeds variable in size and shape, the cells of the testa thin walled, polygonal, with large pits (3–)6–15 μm. across, the embryo with a poorly developed chalazal haustorium. TYPE: *Cladothamnus* Bongard.

GROWTH, MORPHOLOGY, AND ANATOMY

VEGETATIVE ORGANS

GROWTH AND MORPHOLOGY. Like most of the Ericaceae, the four members of the Cladothamneae prefer acid habitats. *Elliottia bracteata*, *E. paniculata*, and *Cladothamnus pyroliflorus* are shrubs less than three meters tall, and, although *E. racemosa* is apparently at least initially a tree, Knight (1938) noted that most plants in the wild are shrubby because they sprout vigorously from the base after damage. All taxa have the same basic architecture: the stems are basically orthotropic, each shoot is terminated

by an inflorescence, and growth is continued by the development of axillary buds. This growth pattern basically conforms to Leeuwenberg's model (nomenclature that of Hallé & Oldeman, 1970) and is similar to that of many Ericaceae, especially the great majority of the subfamily Rhododendroideae (Temple, 1975).

Shoots of the four species can readily be distinguished from one another, even in winter, although the differences between them are mostly trivial. The bark of *Cladothamnus pyroliflorus* begins to exfoliate on twigs that are one year old; this character is not nearly so marked in other species, although in all the phellogen is initiated inside the ring of pericyclic fibers of the stem. *Elliottia paniculata* has sharply angled twigs, the angles being decurrent from the bases of the leaves; the twigs of *E. racemosa* are almost terete (the inflorescence less so); the other two species are intermediate. Not surprisingly, *E. paniculata* has the most prominent foliar buttresses.

The vegetative buds of *Elliottia racemosa* and *Cladothamnus pyroliflorus* consist simply of paired, mucronate bud scales. However, in *E. bracteata*, and even more so in *E. paniculata*, the outer pair of scales does not enclose the mucronate inner scales, so the bud scales are imbricate.

All species have inflorescences terminating the current year's growth, and the terminal buds of vegetative shoots are functional; there is, however, rather surprising variation in the growth patterns of the four species. Often in *Elliottia paniculata*, less frequently in *E. bracteata*, very rarely and perhaps only exceptionally in *E. racemosa*, and never, apparently, in *Cladothamnus pyroliflorus*, growth of the vegetative shoot ceases after a few weeks, and a more or less perulate terminal resting bud, with prominent and well developed scales, is formed (e.g., see Nakai, 1922, under *Tripetaleia paniculata*). Growth soon starts again, and small leaves and an inflorescence are produced (FIGURE 1, D).

In the two other species of the Cladothamneae, *Elliottia racemosa* and *Cladothamnus pyroliflorus*, there is usually no obvious cessation of plant growth, and the foliage leaves and bracts are not clearly distinguishable. However, in *E. racemosa* elongation of the main axis slows down soon after the axis is initiated and then speeds up again. In *E. bracteata* the growth of the inflorescence is frequently similar to that of *C. pyroliflorus* (but see above), although specimens placed in *Elliottia* (*Tripetaleia bracteata* var. *longiracemosa* Nakai) suggest that the transition between vegetative growth and the growth of the inflorescence may sometimes be abrupt (FIGURE 1, B). In these specimens the leafy vegetative shoot has large buds in the axils of the leaves and is rather clearly distinct from the inflorescence, which is long, the lower 4.5–7(–10) cm. of the axis bearing small leaves in the axils of which are neither flowers nor obvious buds. In *E. paniculata* and *E. bracteata* both continuous and discontinuous growth may occur on a single plant during the same season.

The growth pattern of *Elliottia racemosa* and *E. bracteata* has not been observed before in the Ericaceae and may be unique in the family (a comparative study of growth patterns and inflorescence type and develop-

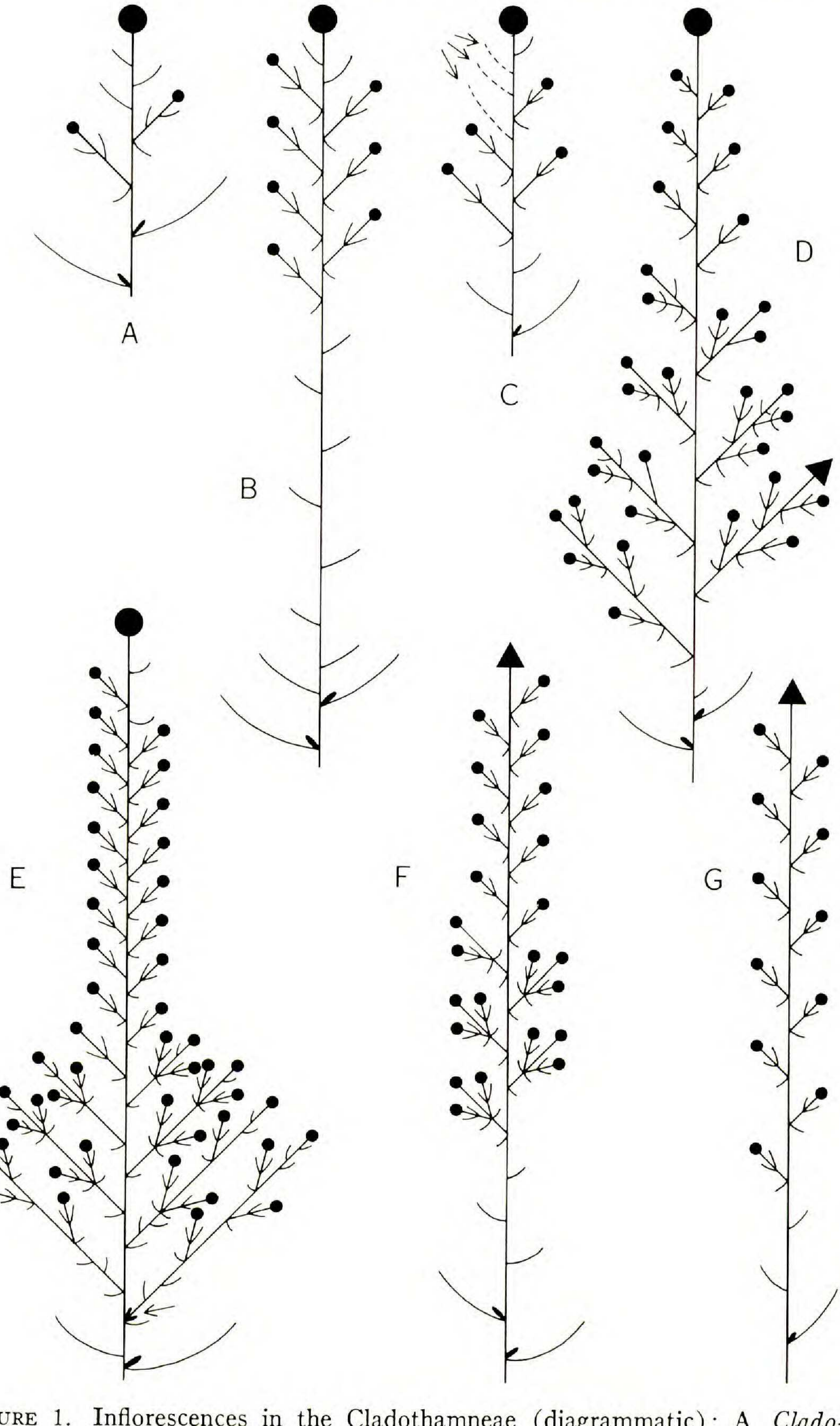

FIGURE 1. Inflorescences in the Cladothamneae (diagrammatic): A, *Cladothamnus pyroliflorus*; B, *Elliottia bracteata* var. *longiracemosa*; C, *E. bracteata* (normal); D, *E. paniculata*; E, *E. bracteata*, unusual branched inflorescence; F, G, *E. racemosa* (circles indicate flowers; ellipses, buds; triangles, axis not obviously terminated by a flower).

ment (see below) throughout the family is much needed). Although Lems's (1962) interesting study of shoot development in the Andromedeae did not include a similar pattern, the closest approach to it seems to be in that tribe. In *Pieris japonica* (Thunb.) D. Don a leafy shoot, a resting bud, and then another leafy shoot terminated by an inflorescence are frequently all produced in the same season; however, the flowers of the inflorescence do not open until the following year (W. Judd, pers. comm.).

All four species of the Cladothamneae are deciduous. (Stevens, 1971, reported that *Elliottia racemosa* was evergreen, but the living plant observed was growing in a greenhouse.) The leaves of *E. racemosa* have long petioles, while those of *Cladothamnus pyroliflorus* are sessile; the other two species have leaves with at most short petioles. Distribution of indumentum and the shape and texture of the leaf blade allow each species to be recognized by its leaf alone (see Key).

ANATOMY. The wood anatomy of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus* was examined by Cox (1948). In this respect, *E. racemosa* was found to be more distinct from the other two species than the two species were from each other. In *E. paniculata* there was a slight preponderance of scalariform perforation plates with more than nine bars, and there were round pits in the wood parenchyma and on the side walls of the vessels. In the other two species there was a strong preponderance of perforation plates with fewer than eight bars, the pits were round or elongate-elliptic, and there were also differences in medullary ray type. *Elliottia racemosa* and *C. pyroliflorus* were similar, differing mainly in the percentage of vessels with porous perforation plates. However, it is difficult to evaluate the significance of these differences since the variation between the species that Cox considered in the natural genus *Befaria* Mutis ex L. was as great as that between the three species of the Cladothamneae that he examined. Perhaps, more importantly, many of the characters that Cox used both vary infraspecifically and also depend on the age and the general health of the part of the plant from which the material examined was taken (see Carlquist, 1961, for references).

The pith of all four species is heterogeneous, with clusters of thick-walled cells interspersed with clusters of larger, thin-walled cells. (Watson, 1965; Stevens, 1971; Gris, 1870, 1872; and Copeland, 1943, give descriptions of the pith that are in basic agreement.) However, the thick-walled cells toward the periphery of the pith tend to be especially well developed. This is particularly marked in *E. paniculata*, in which the pith approaches the *Calluna* type, with small, thick-walled cells in the periphery and larger, thin-walled cells restricted to the center. Copeland (1943) found that in *E. racemosa* most of the pith consisted of thick-walled cells, the thinner-walled cells being relatively inconspicuous.

Stevens (1971) noted that the vascular bundle in the petiole of *Elliottia racemosa* is closed, with the phloem surrounding a ring of xylem, while that of the other species was arcuate. However, in the smaller leaves of *E. racemosa*, especially those produced at the beginning of growth and

those produced later just below the inflorescence, the vascular bundle is open, although it is deeply arcuate. In some intermediate-sized leaves it may be open at the base of the petiole, but then it becomes closed higher up. In the other species it is always shallowly arcuate.

There are a number of differences in lamina anatomy between the four species. Most of these are relatively trivial, and include differences in the thickness of the cuticle, sinuosity of the anticlinal epidermal cell walls (an environmentally labile character), and length of the palisade mesophyll cells. All species have a single layer of palisade cells, although in *Cladothamnus pyroliflorus* and *Elliottia racemosa* there is often a more or less well-developed second layer. The variation in the shape of the midrib bundle mirrors that of the petiole: in *E. racemosa* it is closed to deeply arcuate, while in the other species it is shallowly arcuate. The stomata are always on the abaxial surface of the lamina. In *C. pyroliflorus* and *E. bracteata* the stomata are anomocytic, while in the other two species the majority of stomata are paracytic (Stevens, 1971). The cuticle in *E. bracteata* is almost reticulately ridged, while in the other species it is striate (most prominently so in *E. paniculata*) to smooth.

INFLORESCENCE

STRUCTURE. The inflorescences of the four members of the Cladothamneae are at first sight rather different one from another, and, with the partial exception of *Cladothamnus pyroliflorus*, they have often been called paniculate or racemose (i.e., polytelic: Hooker, 1876; Copeland, 1943; Wood, 1961; Stevens, 1971; Yamazaki, 1975). However, the inflorescences in all four species are basically similar and are more or less clearly monotelic (cymose). In the following discussion, unqualified use of the term "bract" will refer to a leafy structure on the main axis that usually subtends a first-order paracladium (a flower or a more complex, branched system that repeats the structure of the main axis of the flowering system); the bract may be empty. The term "second-order bract" will refer to a comparable structure on a first-order paracladium; and "third-order bract" to a leafy structure borne on a second-order paracladium. (This nomenclature follows that of Troll; see Weberling, 1965, for a convenient summary.)

Cladothamnus pyroliflorus (FIGURE 1, A) has the smallest inflorescence in the Cladothamneae. The 1- to 2- (to 4-)flowered inflorescence, a botrys, has bracts that are almost indistinguishable from the leaves, and any paracladia, which are always single flowers, have a pair of opposite to alternate second-order bracts that are usually called bracteoles because of their position. Between the paracladia and the terminal flower there are usually two or more bracts that do not subtend flowers; small buds are sometimes visible in the axils of these bracts. The terminal flower opens first.

Elliottia bracteata (FIGURE 1, C) has an inflorescence with essentially the same structure as that of *Cladothamnus pyroliflorus*, although the leafy

bracts are smaller and are more clearly distinguishable from the foliage leaves, and the inflorescence is larger, having 3 to 15 flowers. The terminal flower often opens first, although in larger inflorescences the lowest flowers open first, then the terminal flower, and, finally, the remaining ones. Between the two uppermost paracladia there is sometimes a bract lacking an axillant paracladium; this bract is out of phyllotactic sequence, as are any bracts above the uppermost paracladium. In other inflorescences the first bract that does not subtend a paracladium is inserted at, or almost at, the level of the uppermost paracladium, and in yet other inflorescences the first bract is inserted well above the uppermost paracladium (FIGURE 1, C, arrows). In these latter two cases regular phyllotactic sequence is maintained. In the first case the phyllotactic sequence would be regular if the first bract were inserted above the uppermost paracladium, so it seems that this first bract can be variable in position. In some inflorescences there are no empty bracts between the terminal flower and the uppermost paracladium.

Elliottia paniculata has a profuse, branched thyrse that may have over 40 flowers (FIGURE 1, D). The main axis of the inflorescence and the first-order paracladia terminate in flowers that open before the flowers immediately below them. The lower first-order paracladia of the inflorescence bear single flowers along their length and alternate second-order bracts between the terminal flower and the lateral flowers, while the upper first-order paracladia have more or less paired lateral flowers and usually lack second-order bracts between the terminal flower and the uppermost second-order paracladia. Where bracts are present between a terminal flower and a paracladium, they usually continue the phyllotactic spiral of the axis below them, although there is a tendency for the sterile first-order bracts on the main axis to be out of sequence (see above). All second-order paracladia have two subopposite third-order bracts and a terminal flower. The main axis or the first-order paracladium sometimes lacks terminal flowers, and instead there are a number of small bracts of the appropriate order as well as abortive paracladia (axillant flowers). In a few cases none of the paracladia has more than a single flower. When both such variations occur on a single inflorescence (terminal flower lacking only on the main axis), a "racemose" inflorescence results (see below, *E. racemosa*). The lowermost paracladium of one robust inflorescence of *E. bracteata* examined had a pair of second-order bracts, possibly bud scales, at its base (FIGURE 1, E, arrow). Vigorous, branched inflorescences on a plant of *E. bracteata* growing at the Arnold Arboretum were similar in structure to those of *E. paniculata* (FIGURE 1, E).

The main axis of *Elliottia racemosa* is usually not terminated by a flower, but there are a number of bracts subtending abortive paracladia toward the end. The only inflorescences we saw that were terminated by flowers were on a late-flowering plant at the Arnold Arboretum, but they apparently occur sporadically in nature (Wood, 1961, p. 22 (footnote)). The first-order paracladia have either a single terminal flower and two subopposite second-order bracts ("bracteoles": FIGURE 1, F), or two op-

posite second-order paracladia as well, these in turn having a terminal flower and two subopposite third-order bracts (FIGURE 1, G). More complex inflorescences have not been seen, and there are no bracts between terminal flower and paracladium on the lateral branches. The flowers toward the middle of the inflorescence open first (FIGURE 2, A), and the terminal flowers on the three-flowered branches in an inflorescence like that shown in FIGURE 1, G open before the lateral flowers (this latter has been observed before (e.g., Wood, 1961)).

Thus, the inflorescences of all four species are fundamentally monotelic (cymose), although they differ greatly in size and in overall appearance. The small, simple type of inflorescence of *Cladothamnus pyroliflorus* can be related to the more elaborate inflorescences of *Elliottia racemosa* and *E. paniculata* by the lengthening of the main axis, with the terminal flow-

FIGURE 2. Flower types in the Cladothamneae. A, B, *Elliottia racemosa*: A, inflorescence (note flowers in the middle of the inflorescence opening first); B, single flower (note ± erect petals and stamens). C, *E. bracteata* (note more or less spreading petals and stamens); D, *E. paniculata* (note spreading petals and filaments that are initially erect).

er consequently developing later and eventually not developing at all, and the development of both more and also higher orders of paracladia. The inflorescence shows a comparable trend in the reduction of foliation in both the bracts and the sepals. There is also a trend in the regularity of insertion of bracts on paracladia: in *C. pyroliflorus* the bracts tend to be alternate, but in *E. racemosa* they are rather strictly opposite.

Flower

Morphology. There are several differences between the members of the Cladothamneae in the numbers and arrangement of the parts of the flower (see Table 3). Some other floral differences are discussed below.

Calyx. The two species with free sepals, *Elliottia bracteata* and *Cladothamnus pyroliflorus*, also have a very much longer calyx than do the other two species (*E. bracteata*, ca. 5 mm. long; *C. pyroliflorus*, ca. 15 mm. long; *E. paniculata* and *E. racemosa*, less than 2 mm. long).

Corolla color. In *Elliottia racemosa* the petals are white, while in *E. paniculata* and *E. bracteata*, although basically white or pale greenish, they are more or less pink or streaked with pink toward the apex. The petals of *Cladothamnus pyroliflorus* are usually completely copper colored, although they are apparently sometimes greenish white (an albino form?).

Curvature of the stigma and protection of the nectary. Stevens (1971) noted that the petals of *Elliottia bracteata* (Figure 2, C) and *Cladothamnus pyroliflorus* were broadly spreading, as were the stamens. Insects visiting flowers of these species landed on the petals and flattened filaments and received pollen on their backs from that attached to the strongly curved stigma as they took nectar from the exposed nectary at the base of the flower. It was suggested that in *E. racemosa* and *E. paniculata* the pollination mechanism was similar, although it was noticed that petals of the former were not so reflexed; only herbarium material of the latter was seen.

Observations of vigorously growing plants of *Elliottia racemosa* and *E. paniculata* at the Arnold Arboretum show that the style is not strongly recurved and the nectary is not exposed. However, the method of nectar protection differs in the two species. In *E. racemosa* (Figure 2, B; Santamour, 1967, *fig. 54*) the petals are not particularly strongly reflexed and form a cup that encloses the nectary. The edges of the flattened filaments have spaces between them, and the filaments themselves are little bowed at their bases. In *E. paniculata* (Figure 2, D) the petals are reflexed and do not form a cup, but the filaments are bowed at their bases and in contact laterally, thus forming a tube around the base of the ovary and the nectary.

Some details of the pollination of *Elliottia racemosa* were given by Wood (1961), and, although field studies of the pollination of the Cladotham-

neae (and most other Ericaceae) are badly needed, the following additional information based on the plants growing at the Arnold Arboretum seems of interest. No visitors to *E. paniculata* or *E. bracteata* were seen, but numerous bees (*Bombus* and *Apis* spp.) were working *E. racemosa* (see also Santamour, 1967, *fig. 52*). When the pollen is shed in the young bud, it collects in the space between the petals and the stigma (the style is, as yet, short). The style elongates considerably in later bud and, just before the petals open, is compressed into an S-shape. The petals, with their somewhat hooded tips in which the stigma rests, tend to spring open violently when late buds are touched with twigs. Small masses of pollen held together by viscin threads were seen flying through the air when this happened; observations are needed to see if this is an important part of the pollination process. Visiting insects landed on and clung to the petals. The stigma, to which pollen is attached, touched the ventral and lateral surfaces of these insects as they probed for nectar between the filaments; the clefts on the stigmatic lobes are initially closed.

Seeds. The seeds of *Elliottia racemosa* are shieldlike; the embryo and endosperm occupy the central part and are surrounded by a wing composed of testa only (see Wood, 1961, for illustrations). The cells of the testa that forms the wing and that which covers the central part are similar, both having large pitted areas, and are similar to the testa cells of the other members of the Cladothamneae.

Pollen

Methods. For examination under the light microscope, pollen grains were first acetolyzed (Faegri & Iversen, 1964) and were then passed through an alcohol dehydration series before being mounted in silicone oil on glass slides. Measurements for each species were made on specimens from at least two different sources (see TABLE 1). Values were obtained for tetrad diameter, length of the furrow as exposed on the surface of the grain, width of the furrow margin, and exine thickness at the poles of grains.

Both acetolyzed and unacetolyzed pollen samples were prepared for SEM observation. Pollen was air-dried and mounted directly on copper conducting tape that was glued to an aluminum stub. Gold was evaporated onto the material in a Mikros model evaporator, and the stubs were then observed in a Cambridge stereoscan.

Results. The pollen of all four species is borne in tetrads (FIGURE 3, A). The range of tetrad diameter is 40–70 μm. (TABLE 1), with the diameters of these four species forming a series of overlapping ranges. *Elliottia paniculata* has the smallest tetrads, with means between 40 and 45 μm., whereas the other three species have tetrads with means between 40 and 55 μm. However, one of the two samples of *E. racemosa* (*Harper s.n.*) has larger tetrads that vary considerably in size, the mean diameter being 65.6 μm. Tetrad size is especially variable in this species; Santamour

Table 1. Variation in pollen measurements in the Cladothamneae.

	Elliottia bracteata*			Elliottia paniculata+		Elliottia racemosa°		Cladothamnus pyroliflorus++	
	1	2	3	4	5	6	7	8	9
Average tetrad diameter**	51.5	47.8	53.2	42.3	44.7	65.6	52.3	48.0	53.9
Range of tetrad diameter	45-59	44-52	51-57	36-50	42-48	59-74	47-60	42-54	49-57
Standard deviation	2.8	-	-	1.8	-	4.1	-	2.5	-
Sample size	100	10	25	100	10	27	102	100	10
Average grain diameter	35.1	35.2	35.0	30.7	30.0	47.9	37.2	33.0	36.0
Range of grain diameter	29-40	31-39	33-37	25-36	27-32	44-54	33-42	29-38	34-40
Standard deviation	2.1	-	-	2.3	-	3.4	-	2.0	-
Sample size	102	10	10	100	10	8	100	102	10
Furrow length	-	9.9	-	-	8.3	-	9.5	10.2	-
Margin width	-	3.6	-	-	3.9	-	4.3	4.4	-
Average exine thickness	1.2-1.6	1.2-1.6	1.2-2.0	1.6-2.0	1.6-2.0	1.6-2.4	2.0-2.4	2.0-2.4	1.2-2.0
Sample size	10	10	20	10	10	10	10	10	10

*Elliottia bracteata - 1. Bohm, 1975, Garden; 2, Faurie, 1905, Japan; 3, Muroi, 1955, Japan.

+Elliottia paniculata - 4, Bohm, 1975, Garden; 5, Muroi, 1955, Japan.

°Elliottia racemosa - 6, Harper, 1901, Georgia, U.S.A.; 7, Lee, 1960, Georgia, U.S.A.

++Cladothamnus pyroliflorus - 8, Bohm, 1975, B.C., Canada; 9, Peterson, 1959, B.C., Canada.

**All measurements in micrometers (μm.).

(1967) found less than 6 percent fertility in the material that he examined, and the collapse of one or two members of the tetrads was particularly noticeable in this study.

Furrow length (8.3–10.2 μm.) and margin width 3.6–4.4 μm.) are very similar for all four species. A pore extends equatorially to form a fusiform, transverse furrow (FIGURE 3, B) in all members of the group. The wide, differentiated border around the furrow (FIGURE 3, C) is formed mostly by a thickening of the endexine (FIGURE 3, D). This thickened area is surrounded by a peripheral endexinal crack (FIGURE 3, C, surface view; FIGURE 3, B, transverse view) which is usually connected to a network of endocracks (endexinal cracks: FIGURE 3, C) distributed over the visible surface of the grain.

The exine is semitectate, with the ektexine usually from 1.5 to 3 times thicker than the endexine. It consists of a thin foot layer and narrow columellae. Under high magnification both the light micrographs (FIGURE 3, E–H) and SEM micrographs show that the clavobaculate surface ornamentation is produced by the tops of the columellae, some of which are fused (FIGURE 4, B, D, F, H). *Elliottia racemosa* has slightly finer surface ornamentation (FIGURE 4, D) than do the other three species.

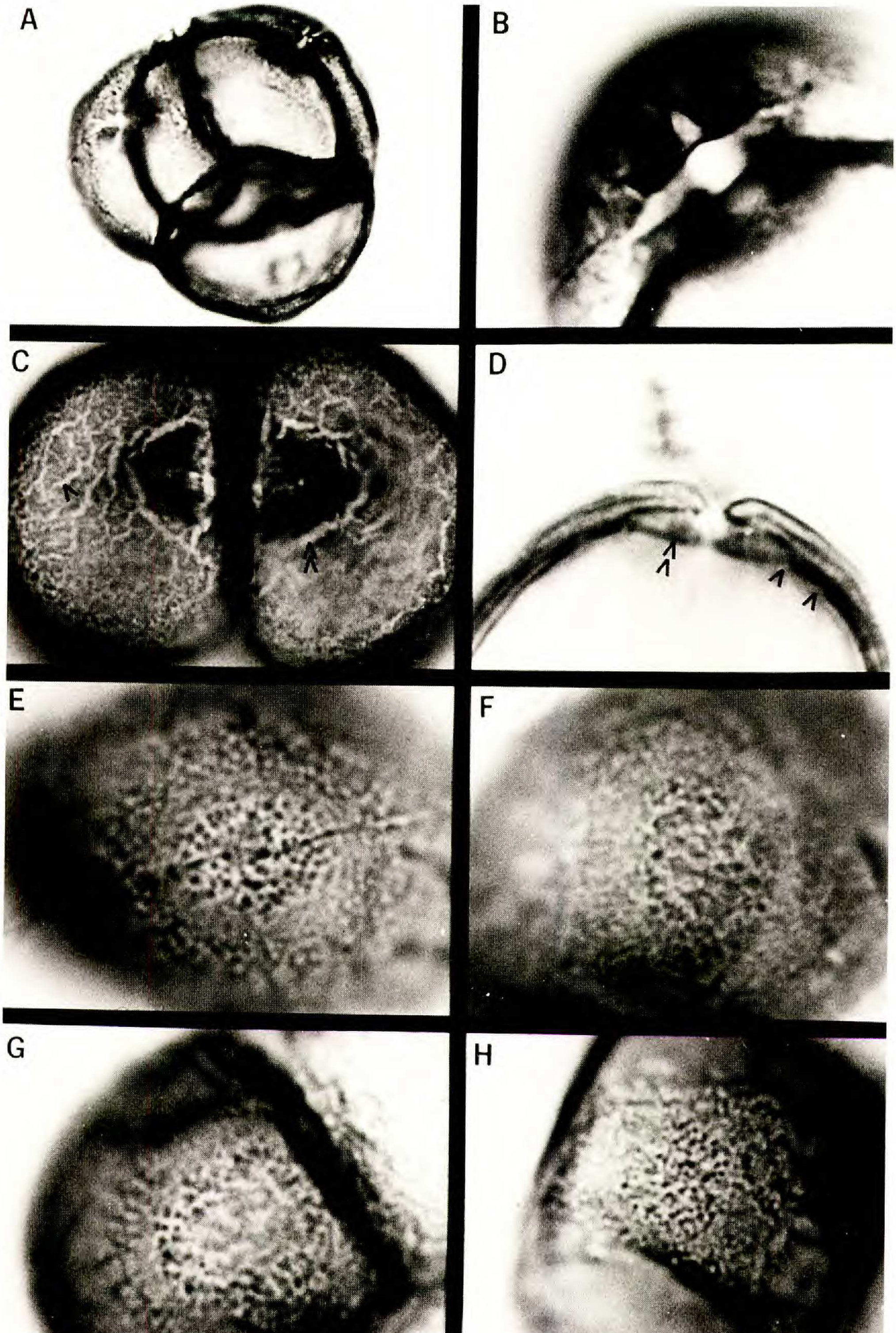

FIGURE 3. Details of pollen of the Cladothamneae. A, *Cladothamnus pyroliflorus*, tetrad, × 760; B, *Elliottia racemosa*, elongate pore crossing furrow, × 2000; C, *Elliottia bracteata*, surface of two adjacent furrows showing differentiated margins, with peripheral endexinal crack (double arrow) surround-

Exine thicknesses of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus* are similar (means, 1.7–2.2 μm.), but the exine of the three collections of *E. bracteata* is somewhat thinner (means, 1.4, 1.4, and 1.5 μm.). Comparison of the SEM micrographs of the unacetolyzed tetrads (FIGURE 4, A, C, E, G) clearly shows that the tetrads of *E. bracteata* collapse much more severely than do those of the other species, probably because of this thinner exine. Collapse can also be seen under the light microscope and has already occurred in herbarium specimens. In some cases acetolysis somehow "reinflated" the grains, destroying the difference between *E. bracteata* and the other species.

The viscin strands observed earlier in the Cladothamneae (e.g., Copeland, 1943) can be clearly seen in the SEM photographs (FIGURE 4, A, C, E, G).

Conclusion. The pollen morphology is very similar in all four species. Although *Elliottia bracteata* has a somewhat thinner exine than do the other species, all of the other essential features are sufficiently similar to indicate very close relationships among the four species. Hence, pollen studies provide no evidence for placing the species in more than one group (see also General Discussion).

Cytology. Santamour (1967) reported a number of $n = 11$ for *Elliottia bracteata*.

Embryology. The chalazal haustoria in *Elliottia racemosa* and *Cladothamnus pyroliflorus* were essentially moribund according to Copeland (1942), and their absence was used to characterize the tribe. However, Yamazaki (1975) found small, but definite, chalazal haustoria in *E. paniculata* and *E. bracteata*. Dissection of mature seeds of *E. bracteata* showed a large micropylar haustorium (pers. obs., P. F. S.), although there was no trace of a chalazal haustorium. All species were reported to have a large micropylar haustorium. Any difference between the species in the size of the micropylar haustorium is probably one of degree only. The micropylar haustorium is much larger than the chalazal haustorium in all three species, whereas in most of the family both haustoria are prominent.

Anatomy. Copeland (1943) examined the floral anatomy of *Elliottia racemosa*, *E. paniculata*, and *Cladothamnus pyroliflorus*. In the first two species he found that there were separate traces to the individual sepals and petals; each of these traces later divided into three. The stamens were likewise supplied by single traces, and the carpels were vascularized by carpel dorsal, carpel ventral, and septal bundles. Branches of the carpel

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ing margins, and reticulum of endexinal cracks (single arrow), × 1248; D, *Elliottia paniculata*, transverse section of furrow, showing endexinal thickening (tip of double arrow) and two endexinal cracks (indentations at tips of single arrows), × 2000. E–H, surface ornamentation, heads of clavobacula showing as black spots, × 2000: E, *C. pyroliflorus*; F, *E. racemosa*; G, *E. paniculata*; H, *E. bracteata*. (For collections examined, see Figure 4.)

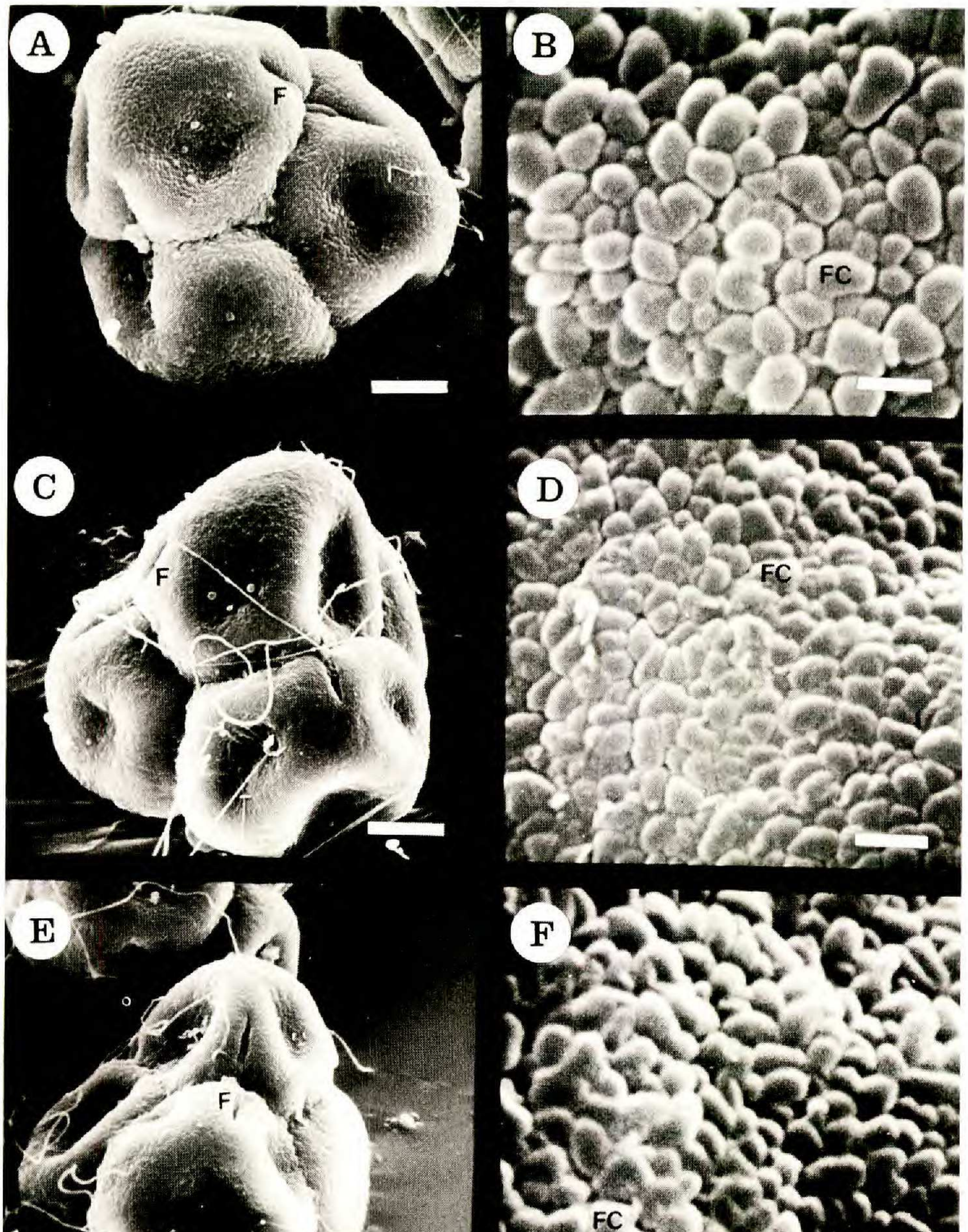

FIGURE 4. Comparison of the pollen of the Cladothamneae. A, C, E, G, scanning electron micrographs of pollen tetrads showing viscin strands and furrows

dorsal and the septal bundles vascularized the nectary. Copeland found *Cladothamnus pyroliflorus* to be basically similar, although its receptacle was depressed and the axis hence more compressed. Up to three vascular bundles supplied the sepals, with the lateral sepal bundles arising from other sepal bundles or from petal bundles, or even originating unattached in the receptacle. The bundles to the antepetalous stamens arose from the petaline bundles, while the vascular bundles supplying the antesepalous stamens sometimes originated from the main sepal bundle. The nectary was not vascularized.

Yamazaki (1975) recently examined the floral anatomy of *Elliottia bracteata* and *E. paniculata* (as *Tripetaleia*). His account disagrees in detail with that of Copeland (1943) and contains a novel suggestion concerning the origin of the petals in these two species. In *E. bracteata* Yamazaki found six petal traces arising from four gaps: two traces from adjacent gaps supplied the adaxial (upper) petal, while a pair of traces arose from each of the two lower gaps and entered the two abaxial (lower) petals. In *E. paniculata* he found that the adaxial petal was supplied by two traces from adjacent gaps, the abaxial petals being vascularized by a single trace that later forked into three. Other details were as given by Copeland (1943). In abortive flowers the upper petals frequently were supplied by a single bundle that forked into two; this bundle arose from a single gap. The vascular supply to the petals of *E. bracteata* suggested to Yamazaki that each petal might have been derived from two by fusion; the vascular supply of *E. paniculata* seemed to him to be more specialized than that of *E. bracteata*.

FLAVONOIDS

A few years ago a study of the flavonoids of the Cladothamneae was undertaken with a view to applying the data to the systematic problems within the tribe. The flavonoids of *Cladothamnus pyroliflorus* were determined at that time (Bohm & Saleh, 1972). Since then, material from the other three taxa has become available. *Cladothamnus* has been reexamined by improved methods, and the structures of the majority of flavonoids present in the other species have been determined.

Several reports of chemical constituents of members of the tribe have been published by other workers. Kondo *et al.* (1963) reported terpene derivatives, paraffins, fatty alcohols, and quercetin from *Tripetaleia paniculata* (= *Elliottia paniculata*). In a series of papers by Yasue and coworkers (1971a, 1971b, 1973, 1974; Sakakibara *et al.*, 1974), a number of long-chain fatty alcohols and ketones, sterol derivatives, simple phenolic

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(F), scale bar = 10 μm.; B, D, F, H, scanning electron micrographs of surface ornamentation of pollen grains, scale bar = 1 μm.: A, B, *Cladothamnus pyroliflorus* (from *Bohm*, 1975, B.C., Canada); C, D, *Elliottia racemosa* (*Lee*, 1960, Georgia, U.S.A.); E, F, *Elliottia paniculata* (*Muroi*, 1955, Japan); G, H, *Elliottia bracteata* (*Bohm*, 1975, garden). Note in G much greater collapse of tetrad in *E. bracteata*; in B, D, F, and H, fused clavobacula (FC).

compounds, and flavonoids were described from various tissues of the same species. The only flavonoid glycosides reported were quercetin 3-O-arabinoside and quercetin 3-O-galactoside. Harborne and Williams (1973) reported kaempferol, quercetin, and myricetin in hydrolyzed extracts of *Cladothamnus pyroliflorus* and *Elliottia racemosa* in their extensive survey of the Ericaceae.

Material. Cladothamnus pyroliflorus was collected in Mt. Seymour Provincial Park, British Columbia, Canada, at the site from which material was obtained for the earlier work on this species (Bohm & Saleh, 1972). *Elliottia racemosa*, from Bulloch Co., Georgia, was supplied by Dr. John Bozeman, of Georgia Southern College, who has retained a voucher specimen. *Elliottia paniculata* was obtained from two sources: 1) Dr. G. Murata, Kyoto University, who collected the material from its native habitat; and 2) my garden (B. A. B.). *Elliotia bracteata* was also available from my garden. Voucher specimens have been prepared; living material of the latter two taxa is being maintained.

Extraction and isolation. Dried material was extracted by repeated soaking with 80 percent methanol, usually with three or four changes of solvent; the extracts were pooled. Fresh material was blended with 80 percent methanol at room temperature in a Waring blender. (The material extracted included leaves, stems, and flowers.) The ground mass was filtered and reextracted with 80 percent methanol by letting it stand, with occasional stirring, for two hours. Three or four changes of solvent gave complete extraction as judged by color loss of the leaf material; the extracts were again pooled and evaporated *in vacuo* at 30°. The resulting aqueous suspension was filtered through a bed of Celite Analytical Filter Aid. Any chlorophyll remaining at this stage was removed by shaking a few times with cyclohexane. The aqueous solution was saturated with NaCl and extracted ten times with ethyl acetate in a separatory funnel. In order to be sure that the more polar constituents had been extracted, two extractions with water-saturated n-butanol were performed. The ethyl acetate and n-butanol extracts were compared by two dimensional thin layer chromatography (TLC); in all cases in this study the two extracts were the same and were combined.

Isolation and purification of the flavonoid glycosides were accomplished by the methods described in detail by Wilkins and Bohm (1976). Structural analyses were based upon standard ultraviolet spectrophotometric methods (Mabry *et al.*, 1970). The proton magnetic resonance (PMR) spectrum of quercetin 3-O-arabinoside (determined as the pertrimethylsilyl ether) was obtained using a Varian HA-100 instrument. Tetramethylsilane was used as the internal standard.

Results. Twenty-two flavonol glycosides have been isolated and identified from the four species examined (TABLE 2). The majority of these compounds are derivatives of kaempferol and quercetin, with quercetin being the major aglycone present in all taxa. Three myricetin glycosides

TABLE 2. **Flavonoid distribution in the Cladothamneae.**

	Cladothamnus pyroliflorus	*Elliottia racemosa*	*Elliottia paniculata*	*Elliottia bracteata*
K-3-O-arabinoside	+	+	+	
3-O-glucoside	+	+	+	+
3-O-galactoside	+	+	+	
3-O-gln	+	+	tr	+
3-O-rha	+			
3-O-rutinoside		+	+	+
3-O-gal-7-O-rha	+			
3-O-ara-7-O-rha	+			
Q-3-O-ara	+[a]	+[a]	+[a]	
3-O-glc	+[a]	+	+[a]	+
3-O-gal	+	+	+	
3-O-gln	+	+	tr	+
3-O-rha		+		
3-O-rutinoside		+	+	+
3-O-rha-ara			+	
0-O-gal-7-O-rha	+			
3-O-ara-7-O-rha	+			
7-O-rha	+			
IR-3-O-rutinoside			+	
M-3-O-ara	+	+	+	
3-O-glc	+	+	+	
3-O-gal			+	

Explanation of abbreviations: K = kaempferol; Q = quercetin; IR = isorhamnetin; M = myricetin; ara = arabinose; glc = glucose; gal = galactose; gln = glucuronic acid; rha = rhamnose; a = isomeric pair of glycosides; + = present; tr = trace only; no entry = absence of compound.

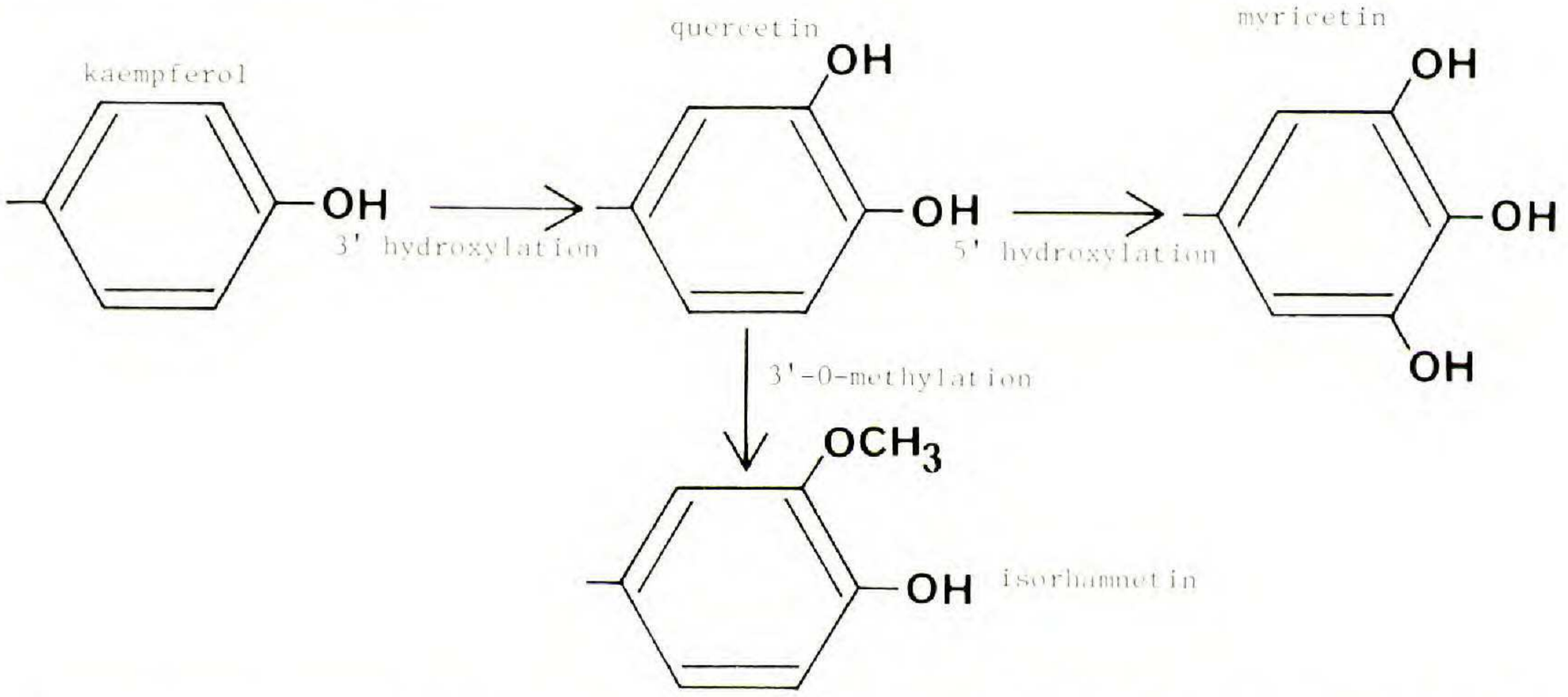
were found. A small amount of isorhamnetin-3-O-rutinoside was found in *Elliottia paniculata*. Within the tribe, *Cladothamnus pyroliflorus* is the only species that makes 3, 7-di-O-glycosides (Bohm & Saleh, 1972). Both kaempferol and quercetin occur as the 3-O-galactosyl-7-O-rhamnosides and 3-O-arabinosyl-7-O-rhamnosides. Reexamination of *C. pyroliflorus* showed a small amount of quercetin-7-O-rhamnoside not noticed before (Bohm & Saleh, 1972).

Three species accumulate pairs of isomeric quercetin-3-O-monosides. *Cladothamnus pyroliflorus* had a pair of quercetin-3-O-arabinosides and a pair of 3-O-glucosides. *Elliottia racemosa* and *E. paniculata* had pairs of 3-O-arabinosides, while *E. paniculata* had a pair of 3-O-glucosides as well. The predominant member of the arabinoside pair from *E. paniculata* was shown to be the β-D-pyranoside by PMR. The predominant member of the glucoside pairs was also the β-D-pyranoside; this was determined on the basis of chromatography against standards known to possess this configuration. In all cases the pyranosides chromatographed more slowly than did the isomeric compounds.

Elliottia paniculata possessed a quercetin-3-O-glycoside derivative that ran in aqueous systems on polyamide plates approximately halfway between the 3-O-glucoside and the 3-O-rutinoside. Total acid hydrolysis yielded quercetin, arabinose, and rhamnose, while partial acid hydrolysis yielded arabinose and a compound indistinguishable from quercetin-3-O-rhamnoside, so the diglycoside is quercetin-3-O-arabinosylrhamnoside. The position of attachment of the "outer" sugar was not determined. Careful search failed to detect this compound in the other taxa.

Discussion. Full use of chemicals for systematic purposes requires knowledge of their biosynthesis and interrelationships. In the case of flavonoids, much is known about the pathways by which the various types are made. Details of some of the steps have been obtained by studying the inheritance of flavonoid pigments and by investigating substrate specificity of enzymes of the pathways. By looking at systems in other plant groups, it is possible to discuss the flavonoid glycoside differences seen in the Cladothamneae in terms of single biochemical steps. Although neither enzymatic nor genetic studies of the Cladothamneae flavonoids have been reported, enough of these other systems is known to suggest that the formation of flavonoids follows much the same route in all plant groups. Some pertinent genetic and enzymatic results are reviewed below.

The formation of the aglycone types found in the Cladothamneae can be summarized by the following abbreviated sequence (flavonol A-rings are omitted for clarity).



It is known that different genes control 3′ and 5′ hydroxylation of anthocyanins as well as flavones and flavonols in several plants (Harborne, 1967). Harborne (1967) also listed several plants in which O-methylation was shown to be controlled by a single gene. Ebel *et al.* (1972) presented evidence showing that specific flavonol O-methyltransferases exist in cultured cells of parsley.

Flavonoid monoglycosides are formed by transfer of the sugar moiety of a nucleoside diphosphate sugar to one of the hydroxyl groups of a flavonoid. Enzymatic and genetic evidence suggest that each such event is under strict control. Using preparations from *Phaseolus vulgaris*, Marsh

(1960) demonstrated the enzymic formation of quercetin 3-O-glucuronide. Similarly, Barber and Chang (1968) showed that an enzyme from *Leucaena glauca* catalyzed the biosynthesis of quercetin 3-O-rhamnoside.

Harborne (1967) has reviewed the genetics of glycosylation reactions in a variety of plants. Typical of the results are the observations of Lawrence and Sturgess (1957) and Harborne (1963) on the inheritance of flower color in *Streptocarpus hybrida*. Separate genes control 3-glycosylation and 5-glycosylation of anthocyanins. Separate genes also control xylosylation to give anthocyanin 3-sambubiosides and rhamnosylation (of 3, 5-diglucosides) to give the 3-rutinoside-5-glucosides. Additional support for the stepwise formation of diglycosides comes from the work of Barber (1962), who showed that the formation of quercetin 3-O-rutinoside occurs in *Phaseolus aureus* by successive enzyme reactions. In recent work with cell cultures of parsley, Sutter and coworkers (Sutter *et al.*, 1972; Sutter & Grisebach, 1973) have shown the existence of two separable glycosylating enzymes with different positional and substrate specificities. Uridine diphosphate glucose (UDP-glucose) : flavone/flavonol 7-O-glucosyltransferase was specific for the 7-position and would not accept 3-O-glycosides as substrates. The second system, UDP-glucose : flavonol 3-O-glucosyltransferase, was specific for the 3-position but would accept flavonol 7-O-glycosides as substrates.

The flavonoid glycosides of the Cladothamneae are based upon the common aglycones kaempferol, quercetin, isorhamnetin, and myricetin (TABLE 2). *Elliottia bracteata* has kaempferol and quercetin glycosides only; *Cladothamnus pyroliflorus* and *E. racemosa* make kaempferol, quercetin, and myricetin glycosides, while *E. paniculata* goes one step further and accumulates the three hydroxy flavonols as well as the O-methylated flavonol isorhamnetin. Thus, on the basis of aglycone elaboration, *E. bracteata* and *E. paniculata* can be distinguished from one another and from the other two taxa, which are indistinguishable.

In the case of monoglycoside composition, *Elliottia bracteata* can be distinguished from the other three taxa by its simplicity, only glucosides and glucuronides being found. The other taxa make both of these, as well as arabinosides and galactosides. *Elliottia racemosa* can be distinguished from the other taxa by its ability to make quercetin 3-O-rhamnoside. *Cladothamnus pyroliflorus* has kaempferol 3-O-rhamnoside and quercetin 7-O-rhamnoside. *Elliottia paniculata* has the capacity to make quercetin 3-O-rhamnoside, but this compound is converted to the 3-O-arabinosylrhamnoside; no monorhamnoside was detected. *Elliottia bracteata* does not make monorhamnosides, but does have the capacity to make rhamnosylglucosides (rutinosides).

Interesting differences exist in the diglycoside fraction of the four species. The three species of *Elliottia* contained 3-O-rutinosides, but *Cladothamnus pyroliflorus* did not. A striking feature of *C. pyroliflorus* is its capacity to make flavonol-3-O-galactoside-7-O-rhamnosides and 3-O-arabinoside-7-O-rhamnosides. It seems reasonable to postulate that this represents a significant difference in rhamnosyltransferase enzymes compared

to the other three members of the tribe. In *Elliottia* rhamnosylation occurs at position 3 of the flavonol or at the 6″ position of the flavonol-3-O-glucosides. *Cladothamnus pyroliflorus* appears to be able to carry out the first of these reactions (it had kaempferol-3-O-rhamnoside), but it does not convert the product further. It can also make the 3-O-glucoside, but further rhamnosylation to the rutinoside does not occur. Finally, *C. pyroliflorus* was found to have quercetin-7-O-rhamnoside, unique in the tribe. In line with the specificity findings of Sutter and coworkers (1972, 1973), this last compound could serve as substrate for enzymes transferring arabinose and galactose to the 3-position of the 7-O-rhamnosides.

One further distinction can be based upon diglycoside data. *Elliottia paniculata* and *E. bracteata* have in common the capacity to synthesize rutinosides, but they can be distinguished from one another on the basis of the formation of quercetin-3-O-arabinosyl-rhamnoside in the former but not in the latter.

GENERAL DISCUSSION

Despite our rather considerable knowledge of the variation in the Cladothamneae, the main points of which are summarized in TABLE 3, the decision as to how many genera should be recognized is still not an easy one. When the Cladothamneae are considered in terms of unique characters or character states that one or more species may have, it is clear that both *Elliottia racemosa* and *Cladothamnus pyroliflorus* are individually more different from the other three species than are *E. bracteata* and *E. paniculata*, although the species pairs *E. bracteata-C. pyroliflorus* and *E. paniculata-E. racemosa* each have a number of characters in common.

Elliottia racemosa differs from all other Cladothamneae in its more or less closed petiole and lamina bundle (and perhaps also in characters of wood anatomy: cf. Cox, 1948), in its inflorescence, which usually lacks a terminal flower, and in its thick-walled capsules with flattened, winged seeds that are shed only tardily. *Cladothamnus pyroliflorus* differs from the other three species in its copper-colored petals, sessile gynoecium, and unvascularized nectary, as well as in several aspects of the flavonoid chemistry (see also TABLE 2). Of the latter, the occurrence of 7-O-rhamnosylation and the associated "diglycoside replacement" is perhaps most important. The species pairs *Elliottia bracteata-Cladothamnus pyroliflorus* and *E. paniculata-E. racemosa* have in common stomatal configuration, calyx size and type, and flower type.

There are numerous other differences in morphology, anatomy, and flavonoid chemistry (aglycone structure and richness and complexity of glycosylation types) that allow the ready recognition of each species and that help to give them their very distinctive individual appearances. These would support the recognition of genera if suggested by other evidence, but of themselves are insufficient to characterize genera. Of greater significance are the numerous characters that all four species have in common, at least some of which might be expected to vary if one were dealing with

Table 3. Variation of some characters among species of the Cladothamneae.

	Elliottia racemosa	Elliottia paniculata	Elliottia bracteata	Cladothamnus pyroliflorus
Two periods of growth per season	-	+(-)	+-	-
Buds with imbricate bud scales	-	++	+	-
Petiole bundle closed or deeply arcuate	+	-	-	-
Stomata without accessory cells	-	-	+	+
Leaves long-petiolate	+	-	-	-
Lamina rounded at the apex, but mucronulate	-	-	+(-)	+
Inflorescences branched	+-	+	-(+)	-
Inflorescences usually with a terminal flower	-(+)	+(-)	+	+
Sepals free, foliaceous	-	-	+	+
Calyx lobe/sepal number	4-5	(3-)5(-6)	(4-)5	5-6
Petal number	4-5	3-4	3	5-6
Corolla basically white	+	+	+	-
Stamen number	8-10	(5-)6-8	5-6	8-10
Gynoecium stipitate	+	++	+	-
Nectary exposed, style curved more than 90°	-	-	+	+
Number of ovules per loculus	8-10	intermediate	numerous	numerous
Capsule thick-walled	+	-	-	-
Seeds strongly flattened and winged	+	-	-	-
Nectary vascularized	+	+	+	-
Myricetin glycosides	+	+	-	+
Isorhamnetin 3-O-rutinoside	-	+	-	-
Monoglycosides - arabinosides and galactosides only	-	-	+	-
Diglycosides - 3-O-rutinosides	+	+	+	-
3, 7-di-O-glycosides	-	-	-	+
Quercetin 7-O-rhammoside	-	-	-	+

Explanation of symbols: + = present; ++ = present, very strongly developed; - = absent; () = uncommon state.

different genera; these characters are summarized in the tribal description in the introduction. The significance of the characters that typify the three groupings above is much vitiated by the basic similarity of all four species. The similarity in the pollen of the four species is perhaps to be expected in the Ericaceae; see the limited amount of variation found by Oldfield (1959) in his study of some European taxa.

Elliottia racemosa, suggested by Stevens (1971) as being distinct, can be recognized only by its long-petiolate leaves, woody capsules, and flat-

tened seeds. The inflorescence is similar in structure to that of *E. paniculata*, and the difference in leaf anatomy can be used only to support a genus otherwise well founded: the variation in leaf anatomy found in the Cladothamneae as a whole is common at the infrageneric level elsewhere in the Ericaceae (e.g., *Befaria*, *Rhododendron*, and *Kalmia*).

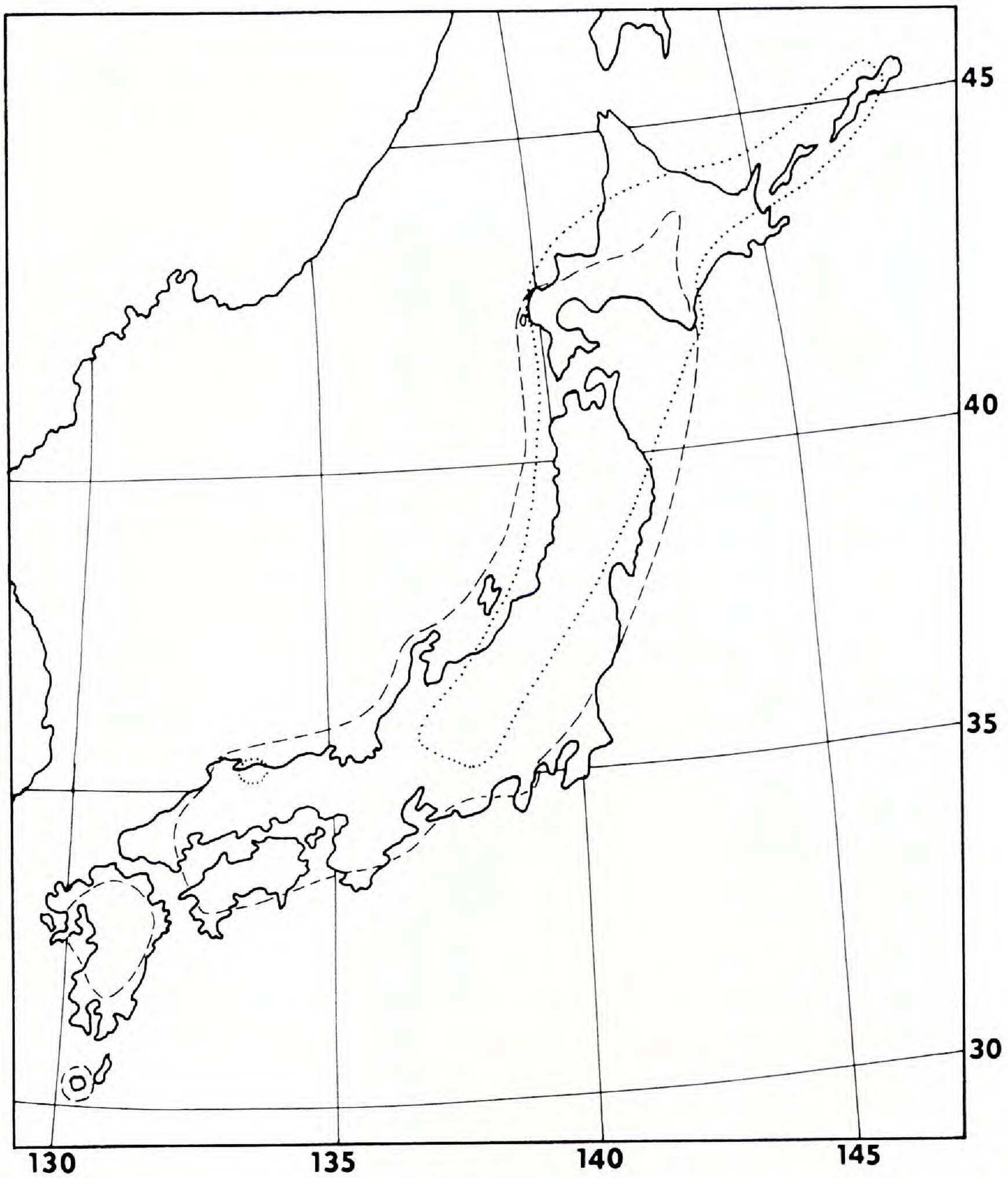
Cladothamnus pyroliflorus is perhaps the most distinctive of the four species in its general appearance. Copeland (1943), following Hooker (1876), distinguished *Cladothamnus* in a key by its sessile leaves that were rounded at the apex, and by its flowers, which were terminal or from the axils of the highest leaves and had 5 or 6 petals (*Elliottia* had petiolate leaves that were acute at the apex, paniculate inflorescences, and flowers often with 3 or 4 petals). It will be clear from TABLE 3 and the preceding discussion that the two latter characters are of little significance; *E. bracteata* has very shortly petiolate leaves that are often broadly rounded and mucronate at the apex and, in these characters, are like leaves of *C. pyroliflorus*. Thus *C. pyroliflorus*, rather like *E. racemosa*, is distinctive mainly because it stands at one end of a number of trends in the Cladothamneae: leaf type, inflorescence elaboration, calyx size, numbers of flower parts. In flower color, sessile gynoecium, and non-vascularized nectary (the last two might be indirectly connected), *C. pyroliflorus* stands somewhat apart from the other Cladothamneae, and it is the only species with a flavonoid chemistry distinctive enough to support generic rank, but the morphological differences are too slight to maintain it as a monotypic genus.

The characters distinguishing *Cladothamnus pyroliflorus* and those distinguishing *Elliottia racemosa* from the rest of the Cladothamneae are rather different. The inflorescence type of *E. racemosa* is clearly derived, and the winged seed also seems to be a specialization of the ellipsoid seed found elsewhere in the Cladothamneae. Flowers in the Ericaceae are basically 5-merous, and the 4-merous flowers of *E. racemosa* with their stipitate gynoecia are probably derived, although less so than those of *E. bracteata* and *E. paniculata*. The closed petiole bundle of *E. racemosa* is possibly less derived than the open condition found in the rest of the genus. In *C. pyroliflorus*, on the other hand, it is possible that only the vegetative characters are derived, and even in these characters *C. pyroliflorus* approaches *E. bracteata*. Unfortunately, not enough is known of the chemical characters to enable discussion concerning whether or not they are derived.

The suggestion that there are two groups in the Cladothamneae, *Elliottia paniculata-E. racemosa* and *E. bracteata-Cladothamnus pyroliflorus*, is a novel one, although Stapf (1934) approached this arrangement when he suggested that his genus *Botryostege* (*E. bracteata*) was closer to *C. pyroliflorus* than to the other two species, which he placed in *Elliottia*. However, it should be remembered that the nectary is protected in different ways in *E. paniculata* (by the bowed filaments) and *E. racemosa* (primarily by the petals). It is also possible that the presence of a large, foliaceous calyx may be functionally correlated with a flat-lying corolla, the large calyx

providing additional support to the platform on which the insects land. In view of the more obvious differences between *E. bracteata* and *C. pyroliflorus*, the recognition of two genera, each with two species, has little to recommend it.

The most satisfactory (or perhaps least unsatisfactory) taxonomic treatment of the Cladothamneae is as a single genus, *Elliottia*, containing four very distinct species that are related in a somewhat reticulate fashion. The names of the species are listed below, and their main synonymy given. Hooker (1876) placed the three species that he included in *Elliottia* (he did not include *Cladothamnus pyroliflorus*) in separate, unnamed sections. Nakai (1922) placed the Japanese species in separate sections with-

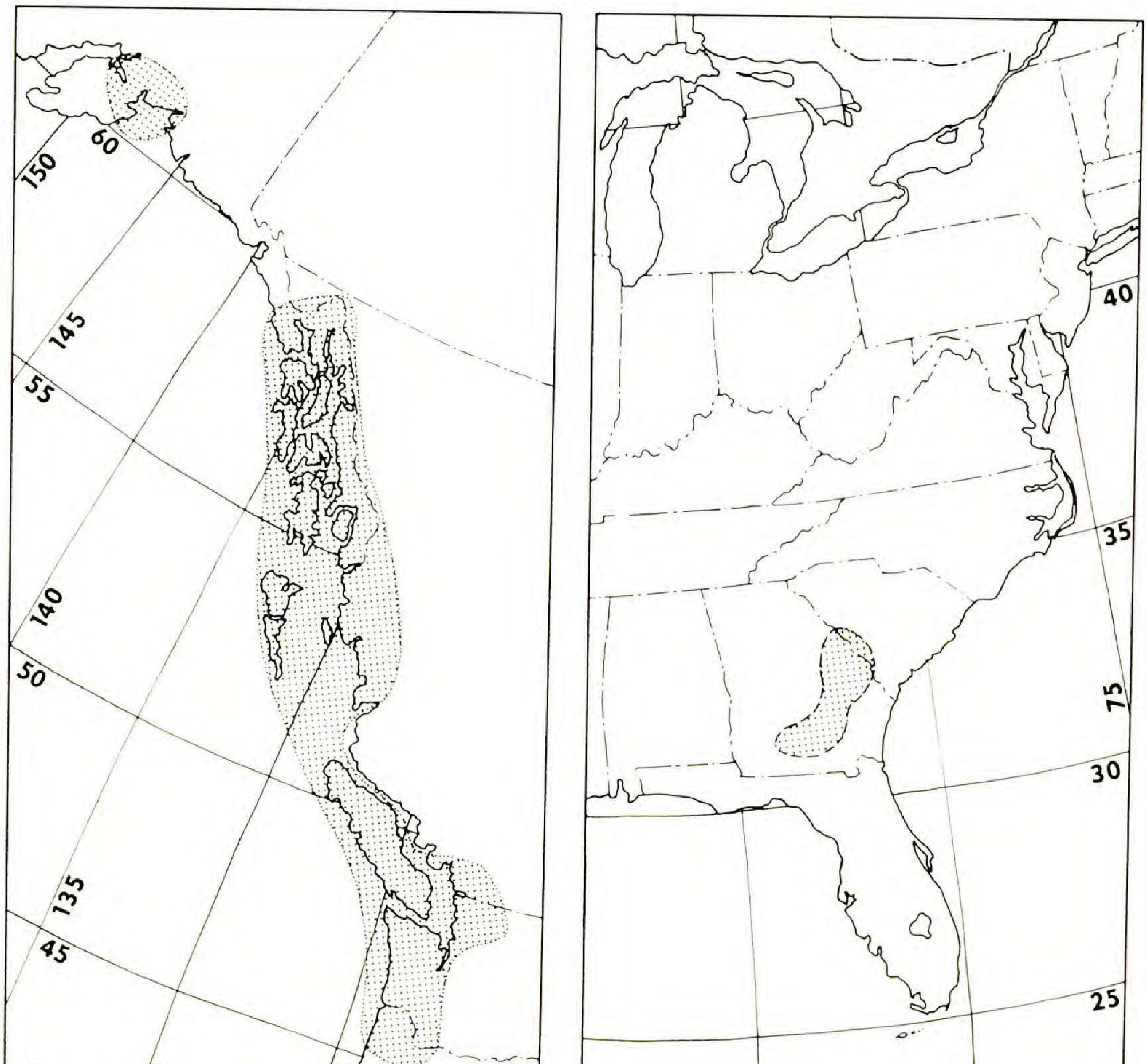


MAP 1. Distribution of *Elliottia* in Japan: dots, *E. bracteata* (from Horikawa, 1972); dashes, *E. paniculata* (from H. Hara, 1958).

in *Tripetaleia*: sect. EUTRIPETALEIA (properly TRIPETALEIA) included *T. paniculata*; sect. SCHIZOCALYX Nakai included *T. bracteata*. The present authors feel that, rather than formally placing each species in a separate section or subgenus, it seems sufficient to remember that all four species are very distinct.

Elliottia as circumscribed here has a disjunct distribution, with *Elliottia bracteata* and *E. paniculata* growing in Japan (MAP 1), *E. pyroliflora* found scattered along the northwest coast of North America from Alaska to Oregon (MAP 2), and *E. racemosa* occurring in the southeastern United States (Georgia and, formerly, South Carolina: MAP 3). This and similar disjunctions (about 50 genera are involved — see Wood, 1972, for references) probably result from the disruption of a widespread early Tertiary flora by climatic change and orogenic events (Graham, 1972).

The four species of *Elliottia* grow in more or less acid and moist habitats, as is common in the Ericaceae. *Elliottia bracteata* grows in grasslands immediately surrounding snowbeds (Ishizuka, 1974) and in mon-



MAPS 2, 3. Distribution of *Elliottia* in North America: 2 (left), *E. pyroliflora* (partly from Hultén, 1968, and Szczawinski, 1962); 3 (right), *E. racemosa*.

tane broadleaf-evergreen forests, and *E. paniculata* grows in similar habitats, but at somewhat lower altitudes. *Elliottia pyroliflora* grows in moist forests, near streams and bogs, along shores, and near the tree line as thickets in openings in hemlock-spruce forests (Calder & Taylor, 1968). *Elliottia racemosa* seems to do best on moist, well-drained sand in mixed woods rather near streams, but it also grows in such habitats as oak-dominated forests, ridges, and *Pinus australis* savannas (Wood, 1961).

Elliottia Muhlenberg ex Elliott, Sketch Bot. South Carolina Georgia 1: 448. 1817.

Cladothamnus Bongard, Mém. Acad. Sci. St.-Pétersb. Sci. Nat. VI. 2: 155. 1832.
Tolmeia Hooker, Fl. Bor.-Am. 2: 44. 1834.
Tripetaleia Siebold & Zuccarini, Abh. Bayer. Akad. Math. Phys. Kl. 3: 731. 1843.
Botryostege Stapf, Kew Bull. **1934**: 194. 1934.

KEY TO THE SPECIES OF ELLIOTTIA

1. Inflorescences usually with fewer than 4 flowers; sepals ca. 15 mm. long; petals copper colored; ovary sessile. ..... 3. *E. pyroliflora.*
1. Inflorescences nearly always with more than 3 flowers; sepals at most ca. 5 mm. long; petals white, tinged with red; ovary stipitate.
   2. Lamina often ± rounded at the apex, mucronate; calyx of free sepals ca. 5 mm. long; nectary exposed in open flower. ..... 1. *E. bracteata.*
   2. Lamina cuneate to acute at the apex, whether or not mucronate; calyx connate, less than 2 mm. long; nectary concealed in open flower.
      3. Twigs subterete; petiole 0.3–1.8 cm. long; capsule woody; seeds flattened. ..... 4. *E. racemosa.*
      3. Twigs strongly angled; petiole less than 4 mm. long; capsule not woody; seeds not flattened. ..... 2. *E. paniculata.*

1. **Elliottia bracteata** (Maximowicz) Hooker f. in Bentham & Hooker f. Gen. Pl. 2: 598. 1876; *Tripetaleia bracteata* Maximowicz, Bull. Acad. Sci. St.-Pétersb. III. 11: 432. 1876; *Botryostege bracteata* (Maximowicz) Stapf, Kew Bull. **1934**: 194. 1934. SYNTYPES: Japan. Yeso [near Hakodate], variis locis, *Maximowicz*; Nambu, 1865, *Tschonoski.*

1a. **Elliottia bracteata** (Maximowicz) Hooker f. forma **bracteata.**

1b. **Elliottia bracteata** (Maximowicz) Hooker f. forma **longiracemosa** (Nakai) Brim & P. F. Stevens, comb. nov.

Tripetaleia bracteata Maximowicz var. *longeracemosa* Nakai, Bot. Mag. Tokyo **44**: 530. 1930; *Botryostege bracteata* (Maximowicz) Stapf forma *longeracemosa* (Nakai) Hara, Bot. Mag. Tokyo **50**: 562. 1936. TYPE: Japan. Yeso, in monte Apoi, prov. Hidaka, *T. Nakai.*

2. **Elliottia paniculata** (Siebold & Zuccarini) Hooker f. in Bentham & Hooker f. Gen. Pl. 2: 598. 1876; *Tripetaleia paniculata* Siebold &

Zuccarini, Abh. Bayer. Akad. Math.-Phys. Kl. 3: 732. 1843. TYPE: Japan, *Siebold*.

T. yakusimensis Nakai, Bot. Mag. Tokyo **40:** 485. 1926. TYPE: Japan. Yakushima, in monte Yaedake, *Kimura*.

3. **Elliottia pyroliflora** (Bongard) Brim & P. F. Stevens, comb. nov.

Cladothamnus pyrolaeflorus Bongard, Mém. Acad. Sci. St.-Pétersb. Sci. Nat. VI. 2: 155. 1832; *Leiophyllum pyrolaeflorum* (Bongard) Dippel, Handb. Laubholzk. 1: 436. 1889. TYPE: [Alaska.] New Archangel, *Mertens*.

Pyrola fruticosa Esch. ex Ledebour, Fl. Ross. 2: 924. 1824. Nomen.[2]

Tolmeia occidentalis Hooker, Fl. Bor.-Am. 2: 44. 1834. TYPE: northwest coast of America, *Menzies*.

4. **Elliottia racemosa** Muhlenberg ex Elliott, Sketch Bot. South Carolina Georgia 1: 448. 1817. SYNTYPES: Georgia. Waynesborough, Burke County, *anon.*; Oconee, *Jackson*.

The reassessment of the generic limits in the Cladothamneae raises some points of more general importance in considering the evolution of the Ericaceae as a whole. *Befaria*, with its terminal inflorescences and polypetalous flowers with large and variable numbers of parts, has often explicitly or implicitly been considered to be the most primitive member of the Rhododendroideae and/or the Ericaceae as a whole (Copeland, 1943, and references; N. Hara, 1958), and the Cladothamneae have been placed close to the Befarieae. Reevaluation of the available evidence shows that there is no necessity to consider *Befaria* and *Elliottia* to be more closely related to each other than to any other Rhododendroideae, and that it is very difficult to assess the position of either genus in any phyletic system of the family.

Although Stebbins (1974, p. 267) cites the Ericaceae as a family in which all members have indeterminate (racemose, polytelic) inflorescences, this is clearly not so; however, monotelic inflorescences seem to be uncommon outside the Cladothamneae. *Befaria racemosa* Vent. (Rhododendroideae - Befarieae) very occasionally has three-flowered branches with a terminal flower, the inflorescence having a structure similar to that shown in FIGURE 1, F (*R. & M. Kral 6715*). In *Ledothamnus* Meissner (Rhododendroideae - Phyllodoceae) there are reports of terminal inflorescences and sometimes single flowers (e.g., Copeland, 1943), but the flowers in the inflorescences examined were all axillary; careful observation is necessary to confirm that the single flowers are truly terminal. In the Vaccinioideae - Andromedeae, *Craibiodendron* W. W. Sm. has flowers apparently terminating the main axes (although these are usually broken off in herbarium specimens) and certainly terminating the lateral axes of

[2] Baillon (Adansonia 1: 197. 1860) described a plant from "California" that Douglas called *Pyrola fruticosa*. Although Baillon clearly considered *P. fruticosa* to be a species of *Cladothamnus*, he did not make the combination of *P. fruticosa* under *Cladothamnus*.

the axillary inflorescences. Occasional terminal flowers occur in *Agarista* D. Don (W. Judd, pers. comm.). Terminal flowers are also reported from the Monotropoideae (Copeland, 1941).

There seems to be a consensus that the cymose, monotelic inflorescence is a more generalized (primitive) type than the racemose, polytelic inflorescence. Although there is some discussion as to whether a single, terminal flower or a three-flowered dichasium is the least specialized inflorescence type of all (see Rickett, 1944; Stebbins, 1974), the few-flowered, highly foliated inflorescence of *Elliottia pyroliflora* (FIGURE 1, A) is either the least specialized type (Rickett, 1944) or very close to it, and can be considered the least specialized type in the Ericaceae as a whole.

The inflorescences are also rather unspecialized in the rest of the genus, but there is apparently a transition to the polytelic inflorescence common in the rest of the family, with a concomitant reduction in foliation, increase in number of flowers, and increase in the regularity of insertion of the highest order bracts (the "bracteoles" of the rest of the family). It is relatively easy to derive at least the great majority of inflorescence types in the Ericaceae from those found in *Elliottia*. The inflorescences of *Befaria* are of a derived type, being usually more compact, less foliated, and apparently almost entirely polytelic; the single exception is noted above.

Much of the other evidence as to the primitiveness of *Befaria* and its close relationship with the Cladothamneae is unsatisfactory. Copeland himself noted (1943) that the extremities of the carpels were more perfectly fused in *Befaria* than in the Cladothamneae, although the vascular bundles supplying the various organs of the flower in *B. racemosa* were all separate (this was not so in the Cladothamneae). There seems to be no reason to consider the reduction of the chalazal haustoria of the embryo in the Cladothamneae to be derived rather than the converse. Copeland considered that the presence of resorption tissue in the anthers and of filaments (viscin threads) in the pollen was evidence of the relationship of *Befaria* and the Cladothamneae, since he thought that such a combination of characters did not occur elsewhere in the Rhododendroideae. However, such a combination also occurs in the Phyllodoceae (Stevens, 1971); the mechanism of anther dehiscence in the Epigeaeae and Diplarcheae is unknown. The presence of an endothecium in the anther of *Befaria* (but not in *Elliottia*) may be an unspecialized character. Although *Befaria* may have more than the 5 sepals, petals, and carpels, and the 10 stamens that are common in the Ericaceae, together with infraspecific variation in the numbers of these organs, this again cannot be considered *a priori* a primitive character; such a combination is a derived state in *Rhododendron* section VIREYA, and species of *Lyonia* that have more than the normal number of floral parts are also derived (W. Judd, pers. comm.). *Elliottia pyroliflora* perhaps has comparable variation in the number of floral organs, although in *Elliottia* as a whole there also seems to be a reduction trend toward trimery, culminating in *Elliottia bracteata*. There are good indications that polypetaly may be a derived character in some Ericaceae (*Ledum*, *Vaccinium* L., and the Pyroloideae: Copeland, 1947; Leins,

1964); the transition from polypetaly to sympetaly in the Ericaceae is clearly neither difficult nor indicative of major phylogenetic differences. Finally, Cox (1948) noted that the wood anatomy of *Befaria* was not notably primitive, and, although he thought that it was rather different from the other Rhododendroideae examined, the evidence given hardly supported such a view.

There are several other differences between the Befarieae and Cladothamneae (Stevens, 1971). *Befaria*, so far as has been examined, has perhaps primitive trilacunar nodes (apparently not constantly so in *B. racemosa*) and tetracytic stomata that are oriented more or less at right angles to the long axis of the leaf; *Elliottia* has unilacunar nodes and anomocytic or paracytic stomata that show no particular orientation. The two differ in leaf vernation, *Befaria* having revolute leaves, *Elliottia* convolute. The entire absence of other than unicellular hairs in *Elliottia* is unusual for the Ericaceae and is perhaps a derived character; *Befaria* has multicellular hairs as well. The testa of *Befaria*, with its elongated, thin-walled cells and very fine pitting, is similar to that of most of the Rhodoreae and some of the Phyllodoceae; that of *Elliottia*, with its broadly pitted, polygonal cells, is unique in the Rhododendroideae. Recent evidence on the distribution of phenolics is also interesting (Harborne & Williams, 1973). The two species of Cladothamneae that they studied were distinct from the other Rhododendroideae in lacking all six phenolic constituents characteristic of that subfamily; *Befaria* was readily characterized by the absence of gossypetin and the predominance of 3, 5-O-methyl flavonols and dihydroflavonols. Harborne and Williams (1973) did not find kaempferol in *Befaria*, although it occurs in all the Cladothamneae.

It is clear that we do not have enough knowledge to talk very constructively about relative advancement in the Rhododendroideae. However, *Befaria* and *Elliottia*, both isolated genera, are clearly not close to one another since they have in common no characters that necessarily suggest immediate relationship. *Befaria* is in some ways (phenolics, inflorescence, indumentum, testa) closer to other Rhododendroideae than is *Elliottia*. Each genus appears to have some "primitive" characters, but the final position of the two genera in any phyletic scheme must take into account both the findings on inflorescence types and those on polypetaly; indeed, all characters must be treated much more critically.

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